Abnormal Dextral Hyperstrophy of Post-Larval *Heliacus*

(Gastropoda: Architeconicidae)

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(Plates 13 and 14)

In 1868, LAGODA described and figured (see Plate 13, fig. 2) a "sinistral," scalariform gastropod shell, naming it (on the plate only) "*Torinia variegata,* LAMARCK, var. *sinistrorsa.*" In this paper we present proof that a similar abnormally coiled "*Torinia*" [=*Heliacus*] (Plate 13, fig. 4) is dextral, and that LAGODA's shell was also dextral.

As the terms are used in this paper, dextrality and sinistrality are not defined with reference to the coiling of the mantle-shell and contained viscera — albeit the apertures of most dextral gastropod shells are "right-handed" and of most sinistral gastropod shells "left-handed." Fundamentally, one is anatomically the mirror image of the other. In dextral forms the primitively paired organs associated with the mantle cavity (ctenidia, osphradia, hypobranchial glands, auricles and kidneys) are reduced or absent (except in some primitive archaeogastropods) on the post-torsional right side, and the anus is displaced to the right. In sinistral forms these paired organs are reduced or absent on the left side, and the anus is displaced to the left. The spires of most dextral gastropod shells project to the post-torsional right side, and the spires of most sinistral shells project to the left (the condition termed orthostrophy) — although an elongate spire may be twisted upwards and posteriad during locomotion. However, some larval and a few post-larval gastropods are dextral but have "left-handed" apertures; their "spires" project to the left (hyperstrophy). In effect, the true spire has become a false umbilicus and the true umbilical area a false spire. Thus, a dextral gastropod shell can superficially appear sinistral (and vice versa) if it is hyperstrophic. For diagrams and further discussion of dextrality, sinistrality, orthostrophy, and hyperstrophy, see KNIGHT (1952, pp. 7 to 9, figure 2).

The protoconchs (≈ larval shells) of some gastropods with orthostrophic teleoconchs (≈ post-larval shells) are hyperstrophic. Such protoconchs are possessed by many opisthobranchs, a few primitive pulmonates, and two families (with living representatives) still classified in the Subclass Prosobranchiata (Streptoneura): Mathildidae and Architectonicidae. [For a study of the hyperstrophic larval shells of the Architectonicidae, see ROBERTSON (in preparation, A)]. All gastropods with hyperstrophic proto-

Explanation of Plate 13

Figure 1: *Heliacus bicanaliculatus* (VALENCIENNES). Normal shell, with orthostrophic teleoconch. South side Bahía San Luis Gonzaga, Baja California Norte, México (West). Intertidal; associated with *Zoanthus danae* (LE CONTE) on sides of rocks. Collected by Dr. Donald R. Shasky, May 28, 1961. A. N. S. P. no. 276232. x 5.

Figure 2: *H. bicanaliculatus.* Abnormal shell, with hyperstrophic teleoconch. "Californie." "*Torinia variegata,* LAMARCK, var. *sinistrorsa*" LAGODA (from LAGODA, 1868). x 5.

Figure 3: *Heliacus cylindricus* (GMELIN). Normal shell, with orthostrophic teleoconch (surface corroded). Tea Table Key, Florida Keys. Collected by Mr. Thomas L. McGinty. A. N. S. P. no. 195956. x 6. See also Plate 14, figs. 1 and 3.

Figure 4: *H. cylindricus.* Abnormal shell, with hyperstrophic teleoconch. Tea Table Key, Florida Keys. Collected by Mr. Frank Lyman, 1938. U. S. N. M. no. 597759. x 6. See also Plate 14, figs. 2 and 4.

Figure 1

Figure 2

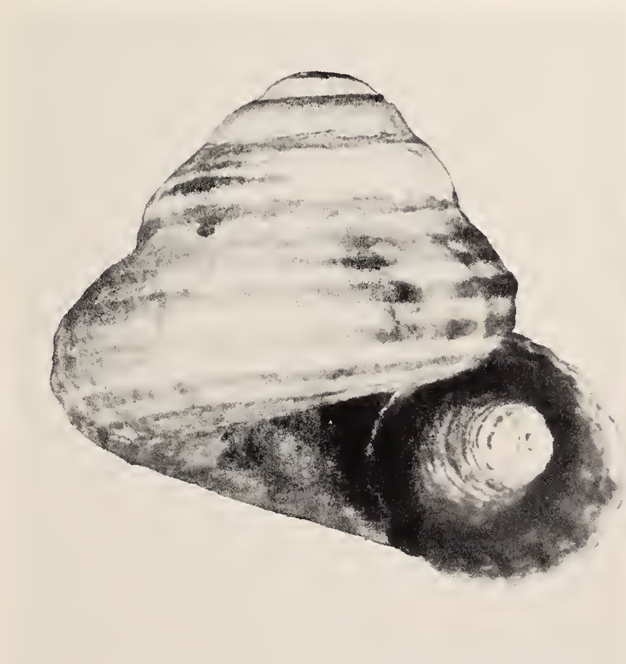

Figure 3

Figure 4

conchs normally are dextral, and the change from hyperstrophic to orthostrophic coiling involves only minor repositioning of the mantle.

Dextrality or sinistrality is determined very early in the embryologic development of every living gastropod, and, once determined, is never reversed; either dextrality or sinistrality is retained thereafter through life. A change from sinistral to dextral (or dextral to sinistral) coiling late in larval life is altogether impossible.

There is no *a priori* reason to exclude the possibility that, abnormally, architectonicid shells may occasionally be sinistral. However, both the protoconch and the teleoconch would have to be sinistral. This profound aberration might or might not affect the normal larval hyperstrophy and post-larval orthostrophy.

A far less profound aberration, not involving sinistrality, would be the abnormal retention of the normal hyperstrophic larval coiling by a post-larval, benthic architectonicid. Such an abnormal shell superficially would appear sinistral if the "spire" were oriented upwards. An architectonicid showing precisely this kind of aberration is illustrated here (Plate 13, fig. 4), together with a normally coiled shell of the same species (Plate 13, fig. 3) from the same locality (Tea Table Key, Florida Keys). This abnormally coiled specimen of *Heliacus cylindricus* (GMELIN, 1791), United States National Museum (U. S. N. M.) no. 597759, can be proved to be dextral and hyperstrophic by using two kinds of evidence: (1) the coiling of the operculum, and (2) the external sculpture of the shell and the form and coloration of the aperture.

PELSENEER (1893) has shown how spiral opercula can be used to distinguish orthostrophic sinistrality from dextral hyperstrophy: viewed externally, spiral opercula of dextral gastropods are coiled counterclockwise, and of sinistral gastropods clockwise. The *Heliacus* operculum is a conical, spiral, and lamellar structure (Plate 13, figs. 3, 4). As can be seen from Plate 14, figures 1 and 2, the coiling of the apices of the opercula in the normal and in the abnormal specimens is counterclockwise.

There are thirteen normal specimens of *Heliacus cylindricus* from Tea Table Key (Florida Keys) in the collection at the Academy of Natural Sciences of Philadelphia (A. N. S. P. nos. 195956, 221378, and 264095). The external sculpture of these shells consists of broad spiral cords separated by sulci. The spiral cords are irregularly wrinkled by axial growth lines. In the umbilicus, the cords and sulci are absent or obscure. Not counting these, there are ten sulci on the last whorl of each of the thirteen shells. There are eleven cords of various widths separated by sulci (including the cord at the periphery of the umbilicus and the irregular cord below the suture). Along the center of some of the sulci there are raised lirae. With the sulci counted clockwise from the suture (Plate 14, fig. 3), lirae most frequently are present in sulci 3 and 5 (on some specimens the lirae are wide enough to resemble narrow cords). Lirae may also be present in sulci 4, 6, and 7, and rarely in sulci 1 and 2. On normal shells, lirae invariably are absent from sulci 8, 9, and 10 (i. e., those on the umbilical half of the base).

Using conchological evidence, it can be shown in three ways that the apertures of the normally and abnormally coiled shells (Plate 14, figs. 3, 4) are both oriented in the same way (i. e., that fig. 4 shows a dextral hyperstrophic shell). On the exterior of the abnormal shell, lirae are present in sulci 2, 3, 4, 5, and 6. If the sulci are counted counterclockwise from the (false) suture (FS), these are sulci v, vi, vii, viii, and ix. Unless the shell is hyperstrophic, the presence of lirae in sulci "8" and "9" is discordant with the normal external sculpture.

The form of the aperture is the second conchological indication that the abnormal shell is properly oriented. The anterior siphonal channel (ASC) is in almost the same position in both apertures. Curiously, in the abnormal shell this channel is opposite the cord between sulci 9 and 10, while on all normal shells it is opposite the cord between sulcus 10 and the umbilicus.

The coloration of the aperture is the third indication of correct orientation. Within, the aperture of the abnormal shell is yellowish brown except the upper left quadrant, the parietal area (PA), where it is white tinged with very pale amber. This area corresponds to the parietal callus of normal shells, which is thinner (affixed to the parietal wall), semitransparent, and white or very pale amber. The parietal area is in the same position in both apertures.

In 1867, more than two decades before the reality of hyperstrophy was conclusively proved, LAGODA not unnaturally assumed that his abnormal "*Torinia variegata*" was sinistral. In a paper in which the concept of hyperstrophy was questioned, FISCHER & BOUVIER (1892, p. 125) included "*Torinia variegata*" in a list of the then known teratologically "sinistral" gastropods. PELSENEER (1893) wrote an elegant paper in rebuttal, one of his series of papers proving the reality of hyperstrophy.

Without discussion, CHARLES BAYER (1948, p. 28) has stated that "*Torinia variegata,* LAMARCK, var. *sinistrorsa* LAGODA" is a "laeotropic [i. e., sinistral] scalarid" [i. e., epitoniid], not a "*Torinia.*" In our opinion this statement is incorrect and there is no reason whatever to question LAGODA's generic identification. LAGODA's shell was white variegated with brown, had the granulated spiral cords of *Heliacus,* and lacked the axial costae possessed by most epitoniids.